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R.O. Xavier, M. B. Leite and D.M. Silva-Matos conceived the ideas and designed the methodology; R.O. Xavier and M. B. Leite collected the data; R. O. Xavier and K. Dexter analysed the data; R. O. Xavier and K. Dexter led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication

ABSTRACT

The impacts of soil properties and fire regime on Neotropical savannas are well-known, but the importance of hydrological regime for plant species assembly has received less attention. Here we assessed changes in diversity patterns of herbaceous and woody communities along a water table gradient in a fire-excluded Neotropical savanna. We found that increased waterlogging of soils was associated with declines in both herbaceous and woody species richness. Woody species richness decreased once the water table depth is less than 4 m and no woody species occurred once water table depth was less than 23 cm. Herbaceous communities remained species rich until the shallowest water table depth, where there is flooding at some point in the year, and even there, over a dozen species occurred. Woody species that occurred in areas with shallower water tables were a nested subset of those in areas with deeper water tables. In contrast, herbaceous communities showed turnover over the hydrological gradient, with distinct species specialised for different water table levels. However, we found that those specialists are restricted to few evolutionary lineages, evidenced by increased phylogenetic clustering over the water table gradient in herbaceous communities. We suggest that evolutionarily conserved hydrological niches define the herbaceous layer over the hydrological gradient, whereas only generalist woody species persist under high water tables. Our findings show that the effect of soil waterlogging differs between the herbaceous and woody layer of savannas, indicating that these communities will respond differently to shifts in the hydrological regime under future environmental change.

Keywords: water table depth, hydrological niches, turnover, phylogenetic.

Introduction

The varying patterns of plant community assembly across environmental gradients have inspired important ecological concepts and have been a recurring subject of research since the earliest ecological studies (Clements 1936; Keddy 1992; Laliberté et al. 2014; Whittaker 1956), and there is increasing interest in understanding plant community assembly in light of ongoing global environmental changes (Lewthwaite et al. 2017). The effects of larger-scale geographic gradients in water availability on community composition and species richness have been demonstrated in a wide range of ecosystems, from tropical forests (Esquivel-Muelbert et al. 2017; Pyke et al. 2001) and seasonally dry ecosystems (Scholes et al. 2002) to riparian forests (Garssen et al. 2015) and floodplains (Casanova and Brock 2000; McGinness et al. 2018; Stevenson et al. 2018). In addition, local variation in hydrological regime can shape plant community composition at individual sites (Araya et al. 2011; Kirkman et al. 2001; Silvertown et al. 1999), which has led researchers to define distinct hydrological niches for different species (Silvertown et al. 2015). However, research in this area has been limited by the difficulty of quantifying hydrological regime. Although assessing soil texture, a proxy for how quickly water percolates through the soil (Wakindiki and Ben-Hur 2002), and topography, which generally relates to the water table depth (Desbarats et al. 2002), is relatively easy, actually measuring water table depth over annual cycles requires substantially more time and financial investment (Morgan and Stolt 2004). Spatial and temporal variation in water tables has been quantified in temperate plant communities, where it is consistently found to have strong effects on plant community composition (Allen-Diaz 1991; Dwire et al. 2006; Shafroth et al. 2000; Silvertown et al. 1999). Similar studies are scarce in the tropics (although see Moulatlet et al. 2014; Targhetta et al. 2015), despite the tropics housing the overwhelming majority of plant diversity.

50 Tropical savannas occur in seasonally dry climates, and typically show a
51 continuous herbaceous layer and a discontinuous woody canopy (Sarmiento 1984).
52 Factors driving the occurrence of savanna *versus* forest have been extensively
53 investigated (de Castro and Kauffman 1998; Sankaran et al. 2005), and recent large-
54 scale studies have highlighted the role of fire regime and herbivory (Hempson et al.
55 2015; Lehmann et al. 2014; Staver et al. 2011). However, seasonal flooding and soil
56 waterlogging, potentially in conjunction with fire occurrence, are also related to the
57 occurrence of savannas in large areas of South America, including the *llanos* of
58 Venezuela and Colombia (Sarmiento and Pinillos 2001), the Rupupuni savannas of
59 Guyana (Eden 1970) and the Llanos de Moxos of Bolivia (Hamilton et al. 2004). There
60 are also extensive areas of hydrologically determined savannas in Brazil (Batalha et al.
61 2005; Cianciaruso et al. 2005; Tannus and Assis 2004), yet most studies of the woody
62 cover and composition of Brazilian savanna have focused on fire regime as a driving
63 variable (Cianciaruso et al. 2012; Moreira 2000; Silva and Batalha 2010).

64 The few studies of hydrological gradients in Brazilian savannas (e.g. Villalobos-
65 Vega et al. 2014, Leite et al 2018) have focused on the woody plant layer, while much
66 of plant species richness of Brazilian savannas lies in the herbaceous layer (Rodrigues
67 Munhoz and Felfili 2007; Tannus and Assis 2004). In fact, herbaceous species can
68 account for over 90% of the plant species richness (Mendonça et al. 1998; Rezende et
69 al. 2008) and most of the primary productivity (Lloyd et al. 2008). In other ecosystems,
70 diversity patterns of herbaceous and woody species are differentially related to
71 environmental variation (Moro et al. 2015; Yan et al. 2013). This is especially expected
72 under distinct hydrological regimes, considering the recurrent differences in water
73 acquisition strategies between herbaceous and woody species (Dodd et al. 1998; Moro
74 et al. 2015; Walter 1979).

In this study, we aimed to assess the effect of water table depth and other abiotic drivers on patterns of species richness and lineage diversity in both woody and herbaceous plant communities along a hydrological gradient in fire-excluded savannas in Southern Brazil, where shallow water tables are thought to be a key driver of open vegetation (Leite et al. 2018). Although both recent fire suppression and past fire regimes are expected to affect current plant community patterns in these savannas, as with any other savanna (Bond and Parr 2010; Brockway and Lewis 1997), the overall study site has experienced little changes in woody cover during the last three decades despite marked variation in woody cover within the site. In other words, the spatial pattern of variation in woody cover has remained relatively static, suggesting that the hydrological regime may be the major force affecting vegetation structure at the site (Leite et al. 2018). Therefore, our study site offers a rare opportunity of investigating the effect of a hydrological gradient on community diversity patterns while controlling for potential additional effects of fire regime.

We specifically aimed to answer the following questions: i) Is the water table depth a major driver of variation in the species richness of plant communities?; ii) Is there turnover in plant species composition along water depth gradients, or are the plant species in more species-poor communities a nested subset of those in more species-rich communities?; iii) Are the plant communities in areas with high water tables comprised of species from few or many evolutionary lineages, i.e. do these plant communities show phylogenetic clustering? iv) Do these patterns differ for herbaceous and woody plant communities? Flooding gradients often lead to high species and phylogenetic turnover in plant communities (Garssen et al. 2015; Silvertown et al. 1999; Tanentzap and Lee 2016), and hence we expect large differences in species and phylogenetic community structure between sites with contrasting hydrological regimes. In addition,

recent research at our study site has demonstrated that the density of the woody layer decreases as water tables become shallower (Leite et al. 2018), so we also expect matching decreases in woody plant species richness. In contrast, we hypothesize that changes in diversity patterns at the herbaceous layer will be present, if at all, along a smaller extent of the water depth gradient, considering that poorly drained Neotropical grasslands and savannas are often species-rich ecosystems (Bueno et al. 2014; Munhoz and Felfili 2006; Killeen and Hinz 1992, Tannus and Assis 2004).

Material and methods

Study site

This study was carried out at the Itirapina Ecological Station (IES), a 2,300 ha protected area in southeast Brazil (Fig. 1a). The local climate is Cwa (Köppen) and the average annual rainfall and temperature during the study period were 1,613 mm and 20.6 °C, respectively (IFSP 2018). There is typically a favourable water balance during the rainy season and a short period of water deficit in the dry season (Xavier et al. 2017). The prevalent soil is an entisol with at least 90% sand (Leite et al. 2018). The IES contains a gradient in vegetation physiognomy that is typical of broader savanna vegetation in Brazil, from grasslands with few shrubs and trees (open savanna - *campo sujo*) to a more closed savanna with higher tree density (dense savanna - cerrado *sensu stricto*) and including an intermediate type (savanna - *campo cerrado*) (Coutinho 1978). The IES maintains some of the last remnants of tropical grasslands in southeast Brazil, where open savannas have been affected by degradation and woody encroachment (Durigan et al. 2007; Stevens et al. 2016). There are no detailed data on the disturbance regime before the IES was established (early 1980s), although the lack of past fire management policies suggest that fire used to occur at the reserve prior to this period.

124 Managers have excluded fire from the IES during the last 25 years. Aerial and satellite
125 imagery taken since the mid-1980s suggest that the distribution of open savannas and
126 grasslands in the IES has changed little during the last 30 years (Leite et al. 2018).

127 We selected 19 sites along a water table depth gradient (Fig. 1a). Vegetation
128 along this gradient varies from wet and marshy grasslands with no woody species to
129 savannas with variable woody cover (campo sujo, campo cerrado and cerrado *sensu*
130 *stricto* – *sensu* Coutinho (1978), Electronic Supplemental Material ESM1). Although
131 we initially aimed to sample an equal the number of sites within each of these three
132 savanna categories, we found that woody cover varies widely within each savanna
133 category (Leite et al. 2018). Likewise, we found that grassland types initially
134 categorized based on visual differences in their flooding regime were in effect
135 distributed along a hydrological gradient, including distinct annual periods of soil
136 waterlogging and standing water (Xavier et al. 2017). Considering these limitations on
137 identifying *a priori* physiognomies or vegetation types at our study site and our aim of
138 assessing community responses to water table depth, our study focus on assessing
139 diversity patterns of woody and plant communities occurring along a continuum of
140 woody cover and hydrological regimes. Sites initially classified into the same
141 vegetation type were always at least 500 m from one another. None of the sites have
142 experienced fire during the last two decades.

143 At each site, we identified and counted all woody individuals with basal
144 diameter greater than 3 cm in six randomly allocated 10 x 10 m plots (Fig. 1b). In order
145 to sample the herbaceous community, in each of these plots we also established six
146 regularly distributed 1 x 1 m subplots spaced 2 m apart, where we identified and
147 counted all individuals of herbaceous species (Fig. 1b, Electronic Supplemental
148 Material ESM2). We assumed that all the stems connected aboveground or at the soil

level belonged to the same individual; turfs of caespitose grasses and sedges with no aboveground connections between them were considered distinct individuals. Individuals were identified to the species level in the field or with further support of previous surveys in the study site, plant collections and consultation with taxonomists (Tannus and Assis 2004). We followed the nomenclature of The Plant List (2017). Unidentified species were classified into morphospecies within genera or families. Across all sites, we could not identify 828 herbaceous individuals to the family level (3.8 % of all herbaceous individuals sampled). Although these individuals were not included in the analysis, most of these morphotypes were single occurrences and hence their absence is unlikely to strongly affect inference on patterns of community assembly at our study sites. Based on these identifications and field observations, species were classified as trees, shrubs or herbs; subshrubs and woody species with no permanent aboveground woody stem were included in the herbaceous layer plant community as they interact primarily with the graminoid and forb species that are typically dominant at this layer. Specimens were deposited in the herbarium of the Federal University of São Carlos, Brazil.

Phylogenetic and Environmental Data

We created a phylogeny that included all species across the plots using the online tool Phylomatic (Webb and Donoghue 2005), based on the Angiosperm Phylogeny Group's APGIII consensus tree (R20120829). Node ages were estimated using the *bladj* algorithm in the software Phylocom 4.2. (Webb et al. 2008) with age constraints from Gastauer et al. (2017). This phylogeny was then pruned to a woody plant species phylogeny and an herbaceous plant species phylogeny, in order to generate separate null expectations for woody and herbaceous plant communities when quantifying phylogenetic community structure.

During the peak of the dry season in 2011 (August), we used a manual auger to drill one 40 mm-wide well down to the groundwater just outside five of the six 10 x 10 m vegetation sampling plots at each site (Electronic Supplemental Material ESM2). At sites where initial drilling showed the water table to be deeper than the maximum drilling capacity of our equipment (7 m), we drilled wells in only two of the six surveyed 10 x 10 m plots. We measured the groundwater depth every two weeks from October 2011 to October 2013 using a Solinst Water Level Meter 102 500' measuring tape. We used the minimum water table depth over this period as an explanatory variable because it represents the maximum waterlogging or highest water table that plants at a given site experience (Xavier et al. 2016). We averaged values across the different plots at a given site. The maximum capacity of the drilling equipment (7.5 m) was used as the minimum water table depth estimate for the sites where the groundwater was too deep to be measured.

We collected 15 soil samples from 0 to 30 cm depth at each study site, which were thoroughly mixed to produce a composite sample by site (see Electronic Supplemental Material ESM3 for the abiotic characterization of each site). Soil texture (sand, silt and clay content) and soil chemical composition (P, N, K, Mg, Al, Ca, pH and organic matter) were obtained following Camargo et al. (2013).

Data analysis

Our main response variables in analyses were the species richness, species diversity and lineage diversity of herbaceous and woody plant communities. Given an equal sample effort in terms of area sampled, our species richness values can be directly compared across sites. To quantify species diversity, we used the Simpson Index (1 – D), which is not only a measure of species richness but also reflects how evenly

198 individuals are distributed across species. Phylogenetic diversity, or the total branch
199 length of a phylogeny comprising the species at a given site, is the most basic measure
200 of lineage diversity; however, this measure is strongly correlated with species richness,
201 and high variation in species richness across communities, as we have at our sites, can
202 obscure any patterns in variation of lineage diversity. We therefore used a null model to
203 calculate the standardized effect size of phylogenetic diversity, based on reshuffling the
204 tips of the phylogeny 1000 times. We refer to this standardized effect size as lineage
205 diversity (c.f. Honorio Coronado et al. 2015; Rezende et al. 2017). It is also a measure
206 of phylogenetic community structure, with negative values reflecting phylogenetic
207 clustering and positive values reflecting phylogenetic overdispersion (Webb et al.
208 2002). We did not use alternative measures of phylogenetic community structure, such
209 as the standardised effect size of the mean phylogenetic distance between species in a
210 community (also referred to as the net relatedness index), because these alternative
211 measures can be highly sensitive to the distribution of species among the three major
212 clades of angiosperms (magnoliids, monocots and eudicots; see Honorio Coronado et al.
213 2015) and our herbaceous and woody plant communities differ substantially in the
214 distribution of their constituent species across these clades. This would therefore
215 complicate comparison of results for woody and herbaceous plant communities.
216 Phylogenetic diversity and its effect size were calculated separately for tree and
217 herbaceous species based on pruned trees comprising only tree and herbaceous species,
218 respectively. These calculations were performed in the R package “picante” (Kembel et
219 al. 2010).

220 Many of our soil variables covary strongly with each other and we therefore
221 used biological reasoning to select a subset of the most pertinent explanatory variables.
222 For example, the abundances of individual base cations are positively correlated with

223 each other, so we used the sum of bases as an explanatory variable in analyses. Also, the
224 soil cation exchange capacity, base saturation, organic matter content and pH were
225 strongly correlated with each other (see Electronic Supplementary Material ESM3 for
226 soil properties from each study site). We included the soil base saturation as an
227 explanatory variable as the variable most likely to be mechanistically related to plant
228 community composition. The minimum water table depth and certain soil properties (N,
229 sum of bases, Al) showed strongly right-skewed distributions in preliminary analyses
230 and were therefore log-transformed prior to linear modelling to reduce
231 heteroscedasticity.

232 We modelled the effect of water table depth and soil properties on species
233 richness, species diversity and lineage diversity using generalized linear models with a
234 negative binomial distribution for species richness (as it represents count data) and a
235 Gaussian distribution for species and lineage diversity. Models were constructed
236 separately for woody and herbaceous plant communities. Explanatory variables were
237 scaled to have the same mean and variance to allow direct comparison of their
238 regression coefficients as a measure of their relative effect on community composition.
239 Given that our overarching aim was to assess the effect of water regime on community
240 composition, we compared the Bayesian Information Criterion (BIC) of models
241 including only water table depth as an explanatory variable with models including water
242 table depth and each of the other soil properties in turn. Limited sample size in terms of
243 study sites (N = 19) prevented us from considering more complex models with more
244 than two explanatory variables, or interactions. However, our approach does serve to
245 test if our results for water table depth are robust to including the major axes of soil
246 variation as covariates. When presenting results, we focus on presenting the best-fitting
247 model for water table depth and one additional soil variable. Semivariograms showed

248 no clear spatial patterns in raw variables or residuals. Further, accounting for spatial
249 autocorrelation did not improve model estimation in generalized linear models
250 (following Zuur et al. 2009), and spatial autocorrelation was therefore not included in
251 the final models presented here.

252 In order to visualise in greater detail how species richness, species diversity and
253 lineage diversity vary with the original non log-transformed water table depth values,
254 we used additive models with thin plate regression splines as smoothing functions with
255 the R package "mgcv" (Wood 2006), without defining a maximum number of basis
256 dimensions. We used this approach because additive models assume no *a priori*
257 relationship between explanatory and response variables (Zuur et al. 2009). Therefore,
258 they are a flexible alternative for identifying ecological thresholds and different types of
259 biologically meaningful non-linear responses (Francesco Ficetola and Denoël 2009;
260 Zuur et al. 2009), which are often found along extensive hydrological gradients such as
261 at our study site (Dwire et al. 2004; Lite and Stromberg 2005).

262 We followed the approach of Leibold and Mikkelson (2002) to assess if there is
263 community turnover or nestedness along the water table gradient, separately for
264 herbaceous and woody plant communities. We sorted the community matrix according
265 to increasing water table depth and calculated the number of times a species was
266 replaced by another between sites with adjacent water table depth; the resulting average
267 turnover value was then compared to the values obtained from 1000 random
268 communities created by permuting the original matrix (Leibold and Mikkelson 2002).
269 Significant differences between these values indicate that the community follows a
270 turnover pattern, whereas similar values suggest a nested pattern. We performed these
271 analyses using the function "Turnover" in the R package "metacom" (Dallas 2014). We
272 also quantified the amount of nestedness in woody and herbaceous plant using the

NODF metric, which is based on decreasing fill and paired overlap in the community matrix (Almeida-Neto et al. 2008). Values obtained for each layer were compared to null expectations based on 30000 random communities that preserved the number of species occurrences and row and column totals (Ulrich et al. 2009). These analyses were performed in the R packages "vegan" (Oksanen et al. 2013) and "bipartite" (Dormann et al. 2008).

Herbaceous and woody morphotypes that could not be identified to the genus or family level were included in nestedness analyses. Matrices for the herbaceous layer included the whole water table gradient, whereas for the woody layer, they only included sites where woody species occurred (11 out of 19 sites). All analyses were performed in the R statistical environment (R_Core_Team 2017), with further support of packages cowplot (Wilke 2016) and ggplot2 (Wickham 2010) for graphic presentation of results.

Results

We identified, at least to the family level, 22,652 individuals from 50 families and 210 species and morphospecies, including 154 herbs and 66 trees. The most common families in terms of abundance and species richness were Myrtaceae, Asteraceae and Fabaceae in the woody layer, and Poaceae and Cyperaceae in the herbaceous layer (see Electronic Supplemental Material ESM3 for species composition at each study site).

Species richness and species diversity were strongly correlated and similarly related to environmental variables, and we therefore only present results for species richness here (see Electronic Supplemental Material ESM4 for results based on species diversity). Species richness and lineage diversity of the herbaceous layer were closely

297 related to water table depth. Most of the best models in terms of BIC values also
298 included soil properties, but the effect of these variables was always smaller than that
299 showed by water table depth and did not affect the sign or significance of the water
300 table depth effect (Table 1). Tree species richness was also strongly related to water
301 table depth and weakly related to soil base saturation, whereas lineage diversity of
302 woody plants was largely unrelated to water table depth or soil factors we measured
303 (Table 1).

304 Generalised additive models (GAMs) showed that the diversity patterns of
305 herbaceous and woody layer had different thresholds of response to water table depth
306 (Fig. 2, Table 2). Although the herbaceous communities on sites subjected to flooding
307 (i.e. negative water table depth) exhibited much lower species richness (points in
308 bottom left of Fig. 2a), additive models only captured a weak linear relationship
309 between water table and species richness. The failure to statistically detect this clearly
310 non-linear relationship is likely related to the very small difference in the measured
311 water table depth values between species-rich grasslands with very shallow water tables
312 and species-poor seasonally flooded grasslands (Fig. 2a). Additive models showed that
313 the lineage diversity of the herbaceous layer increased sharply as water table depth
314 increased until approximately 1 m and remained stable thereafter (Fig. 2c). Woody
315 species richness increased as the water table depth increased to about 4 m, and then
316 showed no clear association with water table depth (Fig. 2b). Woody plant lineage
317 diversity showed no clear relationships with water table depth (Fig. 2d).

318 The community structure of the herbaceous and woody layer also showed
319 different patterns along the water table gradient (Fig. 3). Although certain generalist
320 herb species occurred from grasslands with shallow water table to savannas with deep
321 water table (Fig. 3a), the number of species replacements in the herbaceous layer

between sites with adjacent water table depth was significantly higher than expected according to a null model (z=-4.76 p<0.001), suggesting a turnover pattern. In contrast, the number of replacements in the woody layer did not differ from expected according to a null model (z=0.64, p=0.520), suggesting a nested pattern along the water table gradient (Fig. 3b). Consistent with these findings, the amount of nestedness in the herbaceous layer (NODF=31.10) was significantly lower than expected based on a null model (z=-4.45, p=0.003) and considerably higher than in the woody layer (NODF=49.50), although the amount of nestedness at the woody layer did not differ from the null expectation (z=0.53, p=0.678).

Discussion

Our study shows that seasonally high water tables, which lead to soil waterlogging, have major impacts on both herbaceous and woody plant communities, although the nature of these impacts differs. As shown in previous research at this site (Leite et al. 2018), woody plant species richness declines as water tables become shallower, with no woody plants able to persist as adult trees (> 3 cm diameter at ground level) in areas where the water table comes within 20 cm of the ground surface (see also Fig. 2b). In contrast, many herbaceous species (more than a dozen) can persist at all water table levels, although herbaceous species richness does halve at the shallowest water table depths, where seasonal flooding occurs (Fig. 2a). The herbaceous species that persist at the shallowest water table depths are distinct from those that occur on higher and drier ground (Fig. 3a), and analyses of phylogenetic clustering show that these species come from relatively few evolutionary lineages. In contrast, woody species show a nested pattern of species distributions over hydrological gradients (Fig. 3b), and species occurring at shallower water tables do not seem restricted to particular evolutionary lineages.

347 *Woody communities*

348 As we expected, the richness at the woody layer was severely limited by shallow
349 water table, suggesting intolerance to seasonal waterlogging. The flooding regime often
350 has large effects on riparian woody plant communities (da Paz et al. ; Garssen et al.
351 2015; Garssen et al. 2017), and recent studies have shown a negative effect of shallow
352 water table on the tree species richness of savannas (Villalobos-Vega et al. 2014). We
353 found no trees on sites where the minimum annual water table level was very close to or
354 above the soil surface (i.e. where flooding occurred). These results are somewhat
355 surprising, because in South America many seasonally flooded savannas have been
356 described (Batalha et al. 2005; Bueno et al. 2014; Sarmiento et al. 2004), although these
357 studies did not measure water table depth directly. Considering the negative effects of
358 flooding on plant survival and performance, which require specific adaptations
359 (Mommer et al. 2006), we hypothesize that extended time periods of shallow water
360 tables and flooding are strong abiotic filters that, at least in some areas, cannot be
361 overcome by woody species. Clearly, most tree species present in the species pool for
362 our study area cannot survive such challenging hydrological conditions. We did find
363 that a few tree species could occur where the water table remained a few centimeters
364 deeper than the soil surface, as has been found for other poorly drained Neotropical
365 savannas (Batalha et al. 2005; Bueno et al. 2014). Once water tables were deeper than 3
366 m, we found that minimum water table depth had little effect on tree species richness.
367 Shallow water tables may be buffering open savannas in our study site against woody
368 encroachment associated with fire exclusion, which has been occurring in well-drained
369 Neotropical savannas (Durigan and Ratter 2016; Stevens et al. 2016). However, our
370 findings also show that small changes in the water table dynamics of sites with shallow

water table could have large effects on the species richness of woody plant communities in hydrologically-determined savannas.

Contrasting with the effects on woody species richness, there was no association between water table depth and the lineage diversity of woody communities. Although we found that certain tree species and families (e.g. Myrtaceae, Bignoniaceae, Fabaceae) only occurred where the water table was deeper than 3 m, a few species from multiple lineages (e.g. *Tibouchina stenocarpa*, *Lippia velutina*, *Moquiniastrum polymorphum*) occurred in savannas with both shallow and deep water tables. This is consistent with the complex interaction of anatomical, morphological and physiological adaptations associated with flood-tolerance (Garssen et al. 2015; Kolb and Joly 2009; Kozlowski 1997), which tend not to be phylogenetically clustered (Mommer et al. 2006). Although it is possible that this flooding tolerance generally occurs at taxonomic levels lower than the resolution in our phylogeny (family and genus-level resolution), phylogenies at the same resolution have been used to associate environmental variation and phylogenetic composition (Fine and Kembel 2011; Kubota et al. 2014). In addition, a study based on a fully-resolved phylogeny also found no evidence of phylogenetic clustering along a soil moisture gradient, suggesting that responses to distinct water regimes may be evolutionarily labile in woody plant lineages (Araya et al. 2012). Although assessing if this is a widespread pattern in tropical savannas subjected to high water tables would require investigations at larger spatial scales, our findings suggest that future changes in the hydrological regime in our study site would affect the woody community lineage diversity less than the species richness.

We found that woody species that do occur in areas with high water tables are simply a subset of species from higher and drier areas that have the necessary physiological adaptations to manage this stressful, water-logged environment. Previous

studies also found little turnover of tropical woody species along water availability gradients (Esquivel-Muelbert et al. 2016). In effect, we found that poorly drained savannas were dominated by *Moquiniastrum polymorpha* (Less.) G. Sancho, which also occurs in well-drained areas. This species shows high plasticity in leaf structure, which has been associated with its occurrence in both Neotropical savannas and forests (Rossatto and Kolb 2010). Similarly, certain woody species from the family Melastomataceae, which were common where water tables were high in our study area, are common in Neotropical palm swaps and show leaf anatomy plasticity what seem to favour their occurrence in poorly drained sites (Somavilla and Graciano-Ribeiro 2011). Although plasticity may not be associated with environmental tolerance (Dostál et al. 2016), plasticity on anatomical, physiological and morphological traits, also called low oxygen escape syndrome, allows species without metabolic adaptations to flooding to persist in flood-prone environments (Bailey-Serres and Voesenek 2008). For example, *Sinojackia huangmeiensis* J.W. Ge & X.H. Yao showed distinct seed morphology and composition when subjected to soil waterlogging (Wei et al. 2018). Therefore, phenotypic plasticity, rather than evolutionarily rare adaptations to soil waterlogging, may enable the persistence of these savanna trees species under shallow water tables.

Herbaceous communities

Our data suggest that herbaceous species richness was only reduced over the shallowest water tables, where seasonal flooding occurred. This is expected considering the large negative effect on plant performance and survival of severe soil anoxia and hypoxia associated with flooding, whereas more herbaceous species are expected to occur where there is only seasonal soil waterlogging (Wegner 2010). These findings are consistent with the typically high herbaceous species richness found in other poorly drained Brazilian savannas (Bueno et al. 2014; Munhoz and Felfili 2006; Rodrigues

421 Munhoz and Felfili 2007; Tannus and Assis 2004). Previous studies in temperate
422 grasslands found similar diversity patterns (Dwire et al. 2006), suggesting that
423 seasonally shallow water tables may not be a constraint on herbaceous species richness
424 in a wide range of ecosystems.

425 In contrast to effects on species richness, the lineage diversity of the herbaceous
426 layer was reduced under high water tables. Consistent with this effect, the herbaceous
427 layer of savannas with water tables deeper than 3 m included families (e.g
428 Menispermaceae, Bromeliaceae) absent from sites with shallow water tables. In
429 Neotropical savannas, many perennial herbs and subshrubs are found with relatively
430 large underground structures that support both water uptake and rapid post-fire
431 regeneration (de Castro and Kauffman 1998; Sarmiento 1984). These species may be
432 unable to overcome the hypoxic conditions in sites subjected to soil waterlogging
433 (Bailey-Serres and Voesenek 2008; Pezeshki 2001; Wegner 2010). In our study, these
434 lineages seem to be replaced by a few lineages of small perennial and annual herbs on
435 sites with intermediate water table depth (e.g. Onagraceae, Xyridaceae, Eriocaulaceae),
436 which maintained a high species richness; this likely led to the only slightly lower
437 lineage diversity at these sites compared to the better drained savannas. In contrast,
438 continuous waterlogging and periodic flooding require specific mechanisms to
439 overcome severe soil hypoxia (Bailey-Serres and Voesenek 2008; Kozlowski 1984), so
440 that lineage diversity decreases markedly towards more severe flooding (Tanentzap and
441 Lee 2016). Consistent with this expectation, a few graminoid species and taxa typical
442 from ephemeral wetlands (e.g. *Hidrocotyle*, Maiacaceae) (Deil 2005) occurred in sites
443 subjected to flooding.

444 Differently from the woody layer, we found compositional turnover in the
445 herbaceous layer over the hydrological gradient, possibly because herbaceous and

446 woody plants are differentially affected by high water table. Poor drainage is expected
447 to be a constraint to many cerrado woody species, which often have a deep underground
448 system (Oliveira et al. 2005). Conversely, herbaceous species are often shallow rooted
449 (Rawitscher 1948) and are only expected to be affected by soil waterlogging where the
450 water table is right below the soil surface. In seasonally dry ecosystems, high water
451 tables may even favour the occurrence of herbaceous species with poor tolerance to
452 water deficit, as it may increase the moisture at the superficial soil layer by capillary
453 action (Moore 1939). In effect, there is no annual period of water deficit in most of our
454 study sites subjected to seasonal waterlogging (Xavier et al. 2017). Therefore, we
455 hypothesize that conditions associated with high water tables support specific
456 herbaceous species, and competitive ability is expected to be important for their
457 persistence (Grime 1988). In summary, herbaceous species are most likely to occur
458 where the hydrological regime enables them to perform close to their ecological optima
459 (Silvertown et al. 1999), leading to low niche overlap and species segregation along
460 water table depth gradients (Silvertown et al. 1999). The long-term fire suppression at
461 our study sites has possibly contributed to the emergence of these patterns, as it is
462 expected to favour the most competitive species under different hydrological conditions,
463 to the detriment of generalist and disturbance-prone herbaceous species (Grime 1988;
464 Tilman 1985). Regardless of this possible local effect, our findings highlight the
465 functionally unique composition, and high conservation value, of Neotropical
466 grasslands with high water tables.

467 We conclude that water table depth is the major abiotic factor affecting savanna
468 plant communities at our study site, but this effect varies between the herbaceous and
469 woody layer. There were no trees under hydrological flooding, and only a few woody
470 species, albeit from multiple lineages, persisted at high water tables. Indeed, shallow

water table is a major constraint to the occurrence of tree species in savannas, which may be buffering open savannas in our study site against woody encroachment associated with fire exclusion. Conversely, only actual flooding limited the richness of herbaceous plant communities, whilst high water tables excluded certain lineages and favoured others. For herbaceous plant communities, there was species turnover along the water table depth gradient, consistent with species having distinct hydrological niches. Although further studies should investigate if these diversity patterns are widespread in savanna communities that occur in poorly-drained sites, and how they interact with fire regime, these findings clearly suggest that herbaceous and woody plant communities will respond differently to shifting hydrological regimes under global environmental change.

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Disclosure of potential conflicts of interest

Authors declare no conflict of interest.

496 References
497
498 Allen-Diaz BH (1991) Water table and plant species relationships in Sierra Nevada
499 meadows. American Midland Naturalist 126:30-43
500 Almeida-Neto M, Guimarães P, Guimarães PR, Loyola RD, Ulrich W (2008) A
501 consistent metric for nestedness analysis in ecological systems: reconciling concept
502 and measurement. Oikos 117:1227-1239. doi: 10.1111/j.0030-1299.2008.16644.x
503 Araya YN, Silvertown J, Gowing DJ, McConway KJ, Linder HP, Midgley G (2012) Do
504 niche-structured plant communities exhibit phylogenetic conservatism? A test case
505 in an endemic clade. Journal of Ecology 100:1434-1439.
506 Araya YN, Silvertown J, Gowing DJ, McConway KJ, Linder HP, Midgley G (2011) A
507 fundamental, eco-hydrological basis for niche segregation in plant communities.
508 New Phytologist 189:253-258
509 Bailey-Serres J, Voesenek LACJ (2008) Flooding Stress: Acclimations and Genetic
510 Diversity. Annual Review of Plant Biology 59:313-339. doi:
511 10.1146/annurev.arplant.59.032607.092752
512 Batalha MA, Cianciaruso MV, Silva IA, Delitti WBC (2005) Hyperseasonal cerrado, a
513 new brazilian vegetation form. Brazilian Journal of Biology 65:735-738
514 Bond WJ, Parr CL (2010) Beyond the forest edge: Ecology, diversity and conservation
515 of the grassy biomes. Biological Conservation 143:2395-2404. doi:
516 https://doi.org/10.1016/j.biocon.2009.12.012
517 Brockway DG, Lewis CE (1997) Long-term effects of dormant-season prescribed fire
518 on plant community diversity, structure and productivity in a longleaf pine
519 wiregrass ecosystem. Forest Ecology and Management 96:167-183. doi:
520 https://doi.org/10.1016/S0378-1127(96)03939-4

521 Bueno ML, Damasceno-Junior GA, Pott A, Pontara V, Seleme EP, Fava WS, Salomão
522 AK, Ratter JA (2014) Structure of arboreal and herbaceous strata in a neotropical
523 seasonally flooded monodominant savanna of Tabebuia aurea. Brazilian Journal of
524 Biology 74:325-337
525 Casanova MT, Brock MA (2000) How do depth, duration and frequency of flooding
526 influence the establishment of wetland plant communities? Plant Ecology: 147:237-
527 250
528 Cianciaruso MV, Antônio Batalha M, Aurélio da Silva I (2005) Seasonal variation of a
529 hyperseasonal cerrado in Emas National Park, central Brazil. Flora - Morphology,
530 Distribution, Functional Ecology of Plants 200:345-353. doi:
531 http://dx.doi.org/10.1016/j.flora.2005.02.001
532 Cianciaruso MV, Silva IA, Batalha MA, Gaston KJ, Petchey OL (2012) The influence
533 of fire on phylogenetic and functional structure of woody savannas: Moving from
534 species to individuals. Perspectives in Plant Ecology, Evolution and Systematics
535 14:205-216. doi: https://doi.org/10.1016/j.ppees.2011.11.004
536 Clements FE (1936) Nature and structure of the climax. Journal of ecology 24:252-284
537 Coutinho LM (1978) O conceito do cerrado. Revista Brasileira de Botanica 1:17-23
538 da Paz AA, Ribeiro C, Azevedo AA, de lima ER, da Silva Carmo FM Induced flooding
539 as environemntal filter for riparian tree species. Environmental and Experimental
540 Botany 139: 31-38
541 Dallas T (2014) metacom: an R package for the analysis of metacommunity structure.
542 Ecography 37:402-405
543 de Castro EA, Kauffman JB (1998) Ecosystem structure in the Brazilian Cerrado: a
544 vegetation gradient of aboveground biomass, root mass and consumption by fire.
545 Journal of Tropical Ecology 14:263-283. doi: doi:null

546 Deil U (2005) A review on habitats, plant traits and vegetation of ephemeral wetlands -
547 a global perspective. Phytocoenologia 35:533-706. doi: 10.1127/0340-
548 269X/2005/0035-0533
549 Desbarats AJ, Logan CE, Hinton MJ, Sharpe DR (2002) On the kriging of water table
550 elevations using collateral information from a digital elevation model. Journal of
551 Hydrology 255:25-38. doi: https://doi.org/10.1016/S0022-1694(01)00504-2
552 Dodd MB, Lauenroth WK, Welker JM (1998) Differential water resource use by
553 herbaceous and woody plant life-forms in a shortgrass steppe community.
554 Oecologia 117:504-512. doi: 10.1007/s004420050686
555 Dormann CF, Gruber B, Fründ J (2008) Introducing the bipartite package: analysing
556 ecological networks. R news 8:8-11
557 Dostál P, Fischer M, Chytrý M, Prati D (2016) No evidence for larger leaf trait
558 plasticity in ecological generalists compared to specialists. Journal of
559 Biogeography:n/a-n/a. doi: 10.1111/jbi.12881
560 Durigan G, Siqueira MFd, Franco GADC (2007) Threats to the Cerrado remnants of the
561 state of São Paulo, Brazil. Scientia Agricola 64:355-363
562 Dwire KA, Kauffman JB, Baham JE (2006) Plant species distribution in relation to
563 water-table depth and soil redox potential in montane riparian meadows. Wetlands
564 26:131-146
565 Eden M (1970) Savanna vegetation in the northern Rupununi, Guyana. Journal of
566 Tropical Geography 30:17-28
567 Esquivel-Muelbert A, Baker TR, Dexter KG, Lewis SL, ter Steege H, Lopez-Gonzalez
568 G, Monteagudo Mendoza A, Brienen R, Feldpausch TR, Pitman N, Alonso A
569 (2016) Seasonal drought limits tree species across the Neotropics. Ecography
570 40:618-629. doi: 10.1111/ecog.01904

571 Fine PVA, Kembel SW (2011) Phylogenetic community structure and phylogenetic
572 turnover across space and edaphic gradients in western Amazonian tree
573 communities. Ecography 34:552-565. doi: 10.1111/j.1600-0587.2010.06548.x
574 Francesco Ficetola G, Denoël M (2009) Ecological thresholds: an assessment of
575 methods to identify abrupt changes in species–habitat relationships. Ecography
576 32:1075-1084. doi: 10.1111/j.1600-0587.2009.05571.x
577 Garssen AG, Baattrup-Pedersen A, Voesenek LACJ, Verhoeven JTA, Soons MB (2015)
578 Riparian plant community responses to increased flooding: a meta-analysis. Global
579 Change Biology 21:2881-2890. doi: 10.1111/gcb.12921
580 Garssen AG, Baattrup-Pedersen A, Riis T, Raven BM, Hoffman CC, Verhoeven JT,
581 Soons MB (2017) Effects of increased flooding on riparian vegetation: Field
582 experiments simulating climate change along five European lowland streams.
583 Global change biology 23:3052-3063
584 Grime JP (1988) The CSR model of primary plant strategies—origins, implications and
585 tests. Plant evolutionary biology. Springer, pp 371-393
586 Hamilton SK, Sippel SJ, Melack JM (2004) Seasonal inundation patterns in two large
587 savanna floodplains of South America: the Llanos de Moxos (Bolivia) and the
588 Llanos del Orinoco (Venezuela and Colombia). Hydrological Processes 18:2103-
589 2116. doi: 10.1002/hyp.5559
590 Hempson GP, Archibald S, Bond WJ (2015) A continent-wide assessment of the form
591 and intensity of large mammal herbivory in Africa. Science 350:1056-1061
592 Honorio Coronado EN, Dexter KG, Pennington RT, Chave J, Lewis SL, Alexiades MN,
593 Alvarez E, Alves de Oliveira A, Amaral IL, Araujo-Murakami A, Arets EJ (2015)
594 Phylogenetic diversity of Amazonian tree communities. Diversity and Distributions
595 21:1295-1307

IFSP (2018) Dados meterologicos - Estação Ecologica de Itirapina. Instituto Florestal de São Paulo, http://www.iflorestal.sp.gov.br/Itirapina/dados_metereologicos.html

Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157-164

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463-1464. doi: 10.1093/bioinformatics/btq166

Kirkman LK, Mitchell RJ, Helton RC, Drew MB (2001) Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. American Journal of Botany 88:2119-2128

Kolb RM, Joly CA (2009) Flooding tolerance of Tabebuia cassinoides: Metabolic, morphological and growth responses. Flora - Morphology, Distribution, Functional Ecology of Plants 204:528-535. doi: http://dx.doi.org/10.1016/j.flora.2008.07.004

Kozlowski T (1984) Plant responses to flooding of soil. BioScience 34:162-167

Kozlowski T (1997) Responses of woody plants to flooding and salinity. Tree physiology 17:490

Kubota Y, Hirao T, Fujii S-j, Shiono T, Kusumoto B (2014) Beta diversity of woody plants in the Japanese archipelago: the roles of geohistorical and ecological processes. Journal of Biogeography 41:1267-1276. doi: 10.1111/jbi.12290

Laliberté E, Zemunik G, Turner BL (2014) Environmental filtering explains variation in plant diversity along resource gradients. Science 345:1602-1605

Lehmann CE, Anderson TM, Sankaran M, Higgins SI, Archibald S, Hoffmann WA, Hanan NP, Williams RJ, Fensham RJ, Felfili J, Hutley LB (2014) Savanna Vegetation-Fire-Climate Relationships Differ Among Continents. Science 343:548-552. doi: 10.1126/science.1247355

621 Leibold MA, Mikkelson GM (2002) Coherence, species turnover, and boundary
622 clumping: elements of meta-community structure. Oikos 97:237-250. doi:
623 doi:10.1034/j.1600-0706.2002.970210.x
624 Leite MB, Xavier RO, Oliveira PTS, Silva FKG, Matos DMS (2018) Groundwater
625 depth as a constraint on the woody cover in a Neotropical Savanna. Plant and
626 Soil:1-15
627 Lewthwaite JMM, Debinski DM, Kerr JT (2017) High community turnover and
628 dispersal limitation relative to rapid climate change. Global Ecology and
629 Biogeography 26:459-471. doi: 10.1111/geb.12553
630 Lite SJ, Stromberg JC (2005) Surface water and ground-water thresholds for
631 maintaining Populus–Salix forests, San Pedro River, Arizona. Biological
632 conservation 125:153-167
633 Lloyd J, Bird MI, Vellen L, Miranda AC, Veenendaal EM, Djagbletey G, Miranda HS,
634 Cook G, Farquhar GD (2008) Contributions of woody and herbaceous vegetation to
635 tropical savanna ecosystem productivity: a quasi-global estimate†. Tree Physiology
636 28:451-468. doi: 10.1093/treephys/28.3.451
637 McGinness HM, Arthur AD, Davies M (2018) Flood regimes driving vegetation and
638 bird community transitions in semiarid floodplain woodlands. Ecohydrology
639 11:e1954. doi: doi:10.1002/eco.1954
640 Mendonça RC, Felfili JM, Walter BM, Silva M, Rezende A, Filgueiras TS, Nogueira
641 PE (1998) Flora vascular do cerrado. Cerrado: ambiente e flora. Embrapa-Cpac
642 Planaltina
643 Mommer L, Lenssen JPM, Huber H, Visser EJW, Kroon HD (2006) Ecophysiological
644 determinants of plant performance under flooding: a comparative study of seven

645 plant families. Journal of Ecology 94:1117-1129. doi: doi:10.1111/j.1365-
646 2745.2006.01175.x
647 Moore R (1939) Water conduction from shallow water tables. Hilgardia 12:383-426
648 Moreira AG (2000) Effects of fire protection on savanna structure in Central Brazil.
649 Journal of Biogeography 27:1021-1029. doi: 10.1046/j.1365-2699.2000.00422.x
650 Morgan C, Stolt M (2004) A comparison of several approaches to monitor water-table
651 fluctuations. Soil Science Society of America Journal 68:562-566
652 Moro MF, Silva IA, Araújo FSd, Nic Lughadha E, Meagher TR, Martins FR (2015) The
653 Role of Edaphic Environment and Climate in Structuring Phylogenetic Pattern in
654 Seasonally Dry Tropical Plant Communities. PLOS ONE 10:e0119166. doi:
655 10.1371/journal.pone.0119166
656 Moulatlet GM, Costa FRC, Rennó CD, Emilio T, Schietti J (2014) Local Hydrological
657 Conditions Explain Floristic Composition in Lowland Amazonian Forests.
658 Biotropica 46:395-403. doi: doi:10.1111/btp.12117
659 Munhoz C, Felfili J (2006) Floristics of the herbaceous and subshrub layer of a moist
660 grassland in the Cerrado biosphere reserve (Alto Paraíso de Goiás), Brazil.
661 Edinburgh journal of botany 63:343-354
662 Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL,
663 Solymos P, Stevens MH, Wagner H (2013) vegan: Community Ecology Package. R
664 package version 2.0-10.
665 Oliveira RS, Bezerra L, Davidson EA, Pinto F, Klink CA, Nepstad DC, Moreira A
666 (2005) Deep root function in soil water dynamics in cerrado savannas of central
667 Brazil. Functional Ecology 19:574-581. doi: 10.1111/j.1365-2435.2005.01003.x

668 Pezeshki SR (2001) Wetland plant responses to soil flooding. Environmental and
669 Experimental Botany 46:299-312. doi: https://doi.org/10.1016/S0098-
670 8472(01)00107-1
671 Pyke CR, Condit R, Aguilar S, Lao S (2001) Floristic composition across a climatic
672 gradient in a neotropical lowland forest. Journal of Vegetation Science 12:553-566.
673 doi: 10.2307/3237007
674 R_Core_Team (2017) R: A language and environment for statistical computing. R
675 Foundation for Statistical Computing. Vienna, Austria
676 Rawitscher F (1948) The Water Economy of the Vegetation of the `Campos Cerrados'
677 in Southern Brazil. Journal of Ecology 36:237-268. doi: 10.2307/2256669
678 Mendonça RD, Felfili JM, Walter BM, Silva-Júnior MD, Rezende AV, Filgueiras TD,
679 Nogueira PE, Fagg CW (2008) Flora vascular do bioma cerrado. Cerrado: ecologia
680 e flora. Embrapa, Brasília:1028-1059
681 Rezende VL, Dexter KG, Pennington RT, Oliveira-Filho AT (2017) Geographical
682 variation in the evolutionary diversity of tree communities across southern South
683 America. Journal of Biogeography 44:2365-2375. doi: doi:10.1111/jbi.13013
684 Rodrigues Munhoz CB, Felfili JM (2007) Florística do estrato herbáceo-subarbustivo de
685 um campo limpo úmido em Brasília, Brasil. Biota Neotropica 7
686 Rossatto DR, Kolb RM (2010) Gochnatia polymorpha (Less.) Cabrera (Asteraceae)
687 changes in leaf structure due to differences in light and edaphic conditions. Acta
688 Botanica Brasilica 24:605-612
689 Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J,
690 Higgins SI, Le Roux X, Ludwig F, Ardo J (2005) Determinants of woody cover in
691 African savannas. Nature 438:846

692 Sarmiento G (1984) The Ecology of Neotropical Savannas. Harvard University Press,
693 Cambridge
694 Sarmiento G, Pinillos M (2001) Patterns and processes in a seasonally flooded tropical
695 plain: the Apure Llanos, Venezuela. Journal of Biogeography 28:985-996. doi:
696 10.1046/j.1365-2699.2001.00601.x
697 Sarmiento G, Pinillos M, Silva MP, Acevedo D (2004) Effects of soil water regime and
698 grazing on vegetation diversity and production in a hyperseasonal savanna in the
699 Apure Llanos, Venezuela. Journal of Tropical Ecology 20:209-220
700 Scholes R, Dowty P, Caylor K, Parsons DAB, Frost PGH, Shugart H (2002) Trends in
701 savanna structure and composition along an aridity gradient in the Kalahari. Journal
702 of Vegetation Science 13:419-428
703 Shafroth PB, Stromberg JC, Patten DT (2000) Woody riparian vegetation response to
704 different alluvial water table regimes. Western North American Naturalist:66-76
705 Silva IA, Batalha MA (2010) Phylogenetic structure of Brazilian savannas under
706 different fire regimes. Journal of Vegetation Science 21:1003-1013. doi:
707 doi:10.1111/j.1654-1103.2010.01208.x
708 Silvertown J, Araya Y, Gowing D, Cornwell W (2015) Hydrological niches in terrestrial
709 plant communities: a review. Journal of Ecology 103:93-108. doi:
710 doi:10.1111/1365-2745.12332
711 Silvertown J, Dodd ME, Gowing DJG, Mountford JO (1999) Hydrologically defined
712 niches reveal a basis for species richness in plant communities. Nature 400:61. doi:
713 10.1038/21877
714 Somavilla NS, Graciano-Ribeiro D (2011) Análise comparativa da anatomia foliar de
715 Melastomataceae em ambiente de vereda e cerrado sensu stricto. Acta Botanica
716 Brasilica 25:764-775

717 Staver AC, Archibald S, Levin SA (2011) The Global Extent and Determinants of
718 Savanna and Forest as Alternative Biome States. Science 334:230-232. doi:
719 10.1126/science.1210465
720 Stevens N, Lehmann CER, Murphy BP, Durigan G (2016) Savanna woody
721 encroachment is widespread across three continents. Global Change Biology:n/a-
722 n/a. doi: 10.1111/gcb.13409
723 Stevenson PR, Aldana AM, Cárdenas S, Negret PJ (2018) Flooding and soil
724 composition determine beta diversity of lowland forests in Northern South America.
725 Biotropica 50:568-577. doi: doi:10.1111/btp.12541
726 Tanentzap AJ, Lee WG (2016) Evolutionary conservatism explains increasing
727 relatedness of plant communities along a flooding gradient. New Phytologist:n/a-
728 n/a. doi: 10.1111/nph.14167
729 Tannus JLS, Assis MA (2004) Composição de espécies vasculares de campo sujo e
730 campo úmido em área de cerrado, Itirapina - SP, Brasil. Brazilian Journal of Botany
731 27:489-506
732 Targhetta N, Kesselmeier J, Wittmann F (2015) Effects of the hydroedaphic gradient on
733 tree species composition and aboveground wood biomass of oligotrophic forest
734 ecosystems in the central Amazon basin. Folia Geobotanica 50:185-205. doi:
735 10.1007/s12224-015-9225-9
736 Tilman D (1985) The Resource-Ratio Hypothesis of Plant Succession. The American
737 Naturalist 125:827-852. doi: 10.1086/284382
738 Ulrich W, Almeida-Neto M, Gotelli NJ (2009) A consumer's guide to nestedness
739 analysis. Oikos 118:3-17. doi: 10.1111/j.1600-0706.2008.17053.x
740 Villalobos-Vega R, Salazar A, Miralles-Wilhelm F, Haridasan M, Franco AC, Goldstein
741 G (2014) Do groundwater dynamics drive spatial patterns of tree density and

742 diversity in Neotropical savannas? Journal of Vegetation Science 25:1465-1473.
743 doi: 10.1111/jvs.12194
744 Wakindiki I, Ben-Hur M (2002) Soil mineralogy and texture effects on crust
745 micromorphology, infiltration, and erosion. Soil Science Society of America Journal
746 66:897-905
747 Walter H (1979) Vegetation of the Earth and Ecological Systems of the Geo-Biosphere.,
748 Second Edition edn. Springer Verlag, Berlin-Heidelberg, New York
749 Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: software for the analysis of
750 phylogenetic community structure and trait evolution. Bioinformatics 24:2098-2100
751 Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and
752 community ecology. Annual Review of Ecology and Systematics 33:475-505
753 Webb CO, Donoghue MJ (2005) Phylomatic: tree assembly for applied phylogenetics.
754 Molecular Ecology Resources 5:181-183
755 Wegner LH (2010) Oxigen trasport in waterlogged plants. In: Mancuso SC, S. (ed)
756 Waterlogging Signalling and tolerance in Plants. Springer, Berlin
757 Wei X, Liu M, Wang S, Jiang M (2018) Seed morphological traits and seed element
758 concentrations of an endangered tree species displayed contrasting responses to
759 waterlogging induced by extreme precipitation. Flora 246-247:19-25. doi:
760 https://doi.org/10.1016/j.flora.2018.07.001
761 Whittaker RH (1956) Vegetation of the Great Smoky Mountains. Ecological
762 Monographs 26:1-80. doi: 10.2307/1943577
763 Wickham H (2010) ggplot2: elegant graphics for data analysis. J Stat Softw 35:65-88
764 Wilke CO (2016) cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'.
765 R package version 0.7. 0
766 Wood S (2006) Generalized Additive Models: An Introduction with R. CRC Press

767 Xavier RdO, Leite MB, da Silva-Matos DM (2016) Stress responses of native and
768 exotic grasses in a Neotropical savanna predict impacts of global change on
769 invasion spread. Austral Ecology:n/a-n/a. doi: 10.1111/aec.12475
770 Xavier RO, Leite MB, da Silva-Matos DM (2017) Stress responses of native and exotic
771 grasses in a Neotropical savanna predict impacts of global change on invasion
772 spread. Austral Ecology 42:562-576
773 Yan Y, Yang X, Tang Z (2013) Patterns of species diversity and phylogenetic structure
774 of vascular plants on the Qinghai-Tibetan Plateau. Ecology and Evolution 3:4584-
775 4595. doi: doi:10.1002/ece3.847
776 Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and
777 extensions in ecology with R. Springer, Berlin
778
779
780
781
782
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785
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Tables

Table 1. The effect of water table depth and the most significant additional soil property (in terms of model fit) on the local species richness and phylogenetic clustering of the herbaceous and woody layer in savannas in southeast Brazil, using the generalized linear models. Models assumed negative binomial and Gaussian distributions, respectively.* -p<0.05, **p<0.01, ***p<0.001

Model	Fixed effects	Estimate	SE	*t*
Species Richness				
Herbaceous layer	log(water table depth)	0.20	0.06	3.65***
	soil P	-0.10	0.05	-1.90
Woody layer	log(water table depth)	2.09	0.30	6.97***
	soil P	-0.38	0.19	1.98*
Lineage Diversity				
Herbaceous layer	log(water table depth)	0.83	0.21	3.97***
	base saturation	0.37	0.21	1.78
Woody layer	log(water table depth)	-0.26	0.19	-1.39

Table 2. Results of the generalized additive models estimating the effect of groundwater depth on the local species richness and phylogenetic clustering of the herbaceous and woody layer in savannas in southeast Brazil. Models estimating effects on richness and lineage diversity assumed negative binomial distribution and Gaussian distributions, respectively. edf - effective degrees of freedom. * -p<0.05, **p<0.01, ***p<0.001

Model	edf	Chi.sq/F	R^2 adj
Richness			
Herbaceous layer	1.00	5.14*	0.24
Woody layer	3.55	75.8***	0.88
Lineage diversity			
Herbaceous layer	5.32	13.61***	0.82
Woody layer	1.00	0.00	-0.11

792 **Figure legends**

793 **Fig 1.** Study site and experimental design. a) Satellite image of the Itirapina Ecological
794 Station showing each of the 19 study sites, including marshy grasslands (rhombuses),
795 wet grasslands (crosses) and savannas with low (squares), intermediate (triangles) and
796 high (circles) woody cover. b) Design of a study site with the six 10 x 10 m sample
797 plots (woody layer sampling) and detail of a plot with six the 1 x 1 m subplots
798 (herbaceous layer sampling).

799 **Fig 2.** Relationship between species richness and lineage diversity of the herbaceous
800 a,c) and woody layer b,d) and the water table depth in a Neotropical savanna in
801 southeast Brazil. Negative values of lineage diversity indicate phylogeneetic clustering
802 and positive values indicate phylogenetic overdispersion. Lines are predicted values
803 based on the results of generalized additive models and dashed lines indicate 95%
804 confidence intervals

805 **Fig 3.** Occurrence of a) herbaceous and b) woody species along a water table depth
806 gradient in Southeast Brazil, highlighting the distinct pattern of changes in species
807 composition shown by herbaceous (turnover) and woody plant communities
808 (nestedness). Species of each layer are ranked by their average water table occurrence
809 ((minimum water table depth occurrence + maximum water table depth occurrence) / 2).

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Fig 1.

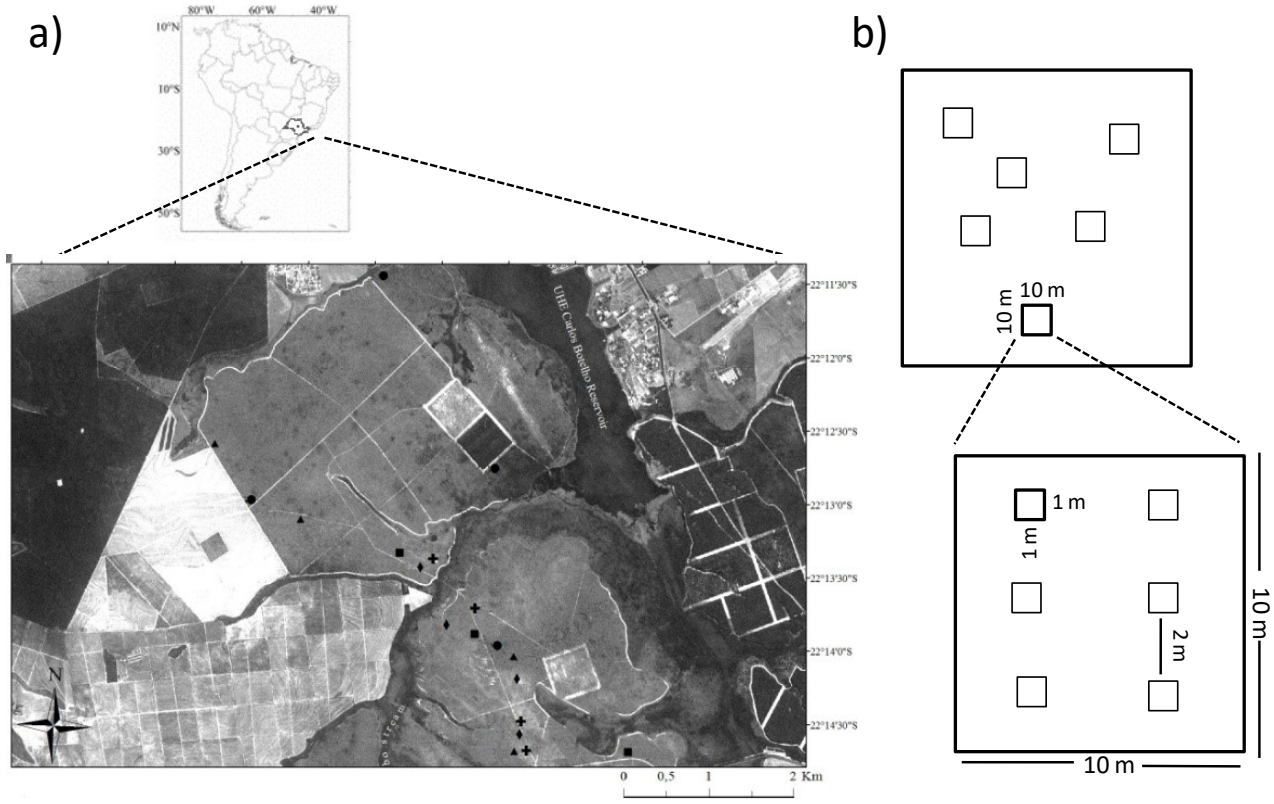

a)
80°W
60°W
40°W
10°N
10°S
30°S
50°S
Utlf Cadeia Boatilho Reservoir
22°11'30"S
22°12'0"S
22°12'30"S
22°13'0"S
22°13'30"S
22°14'0"S
22°14'30"S
N
0
0,5
1
2 Km
b)
10 m
10 m
1 m
1 m
2 m
10 m
10 m

Fig 2.

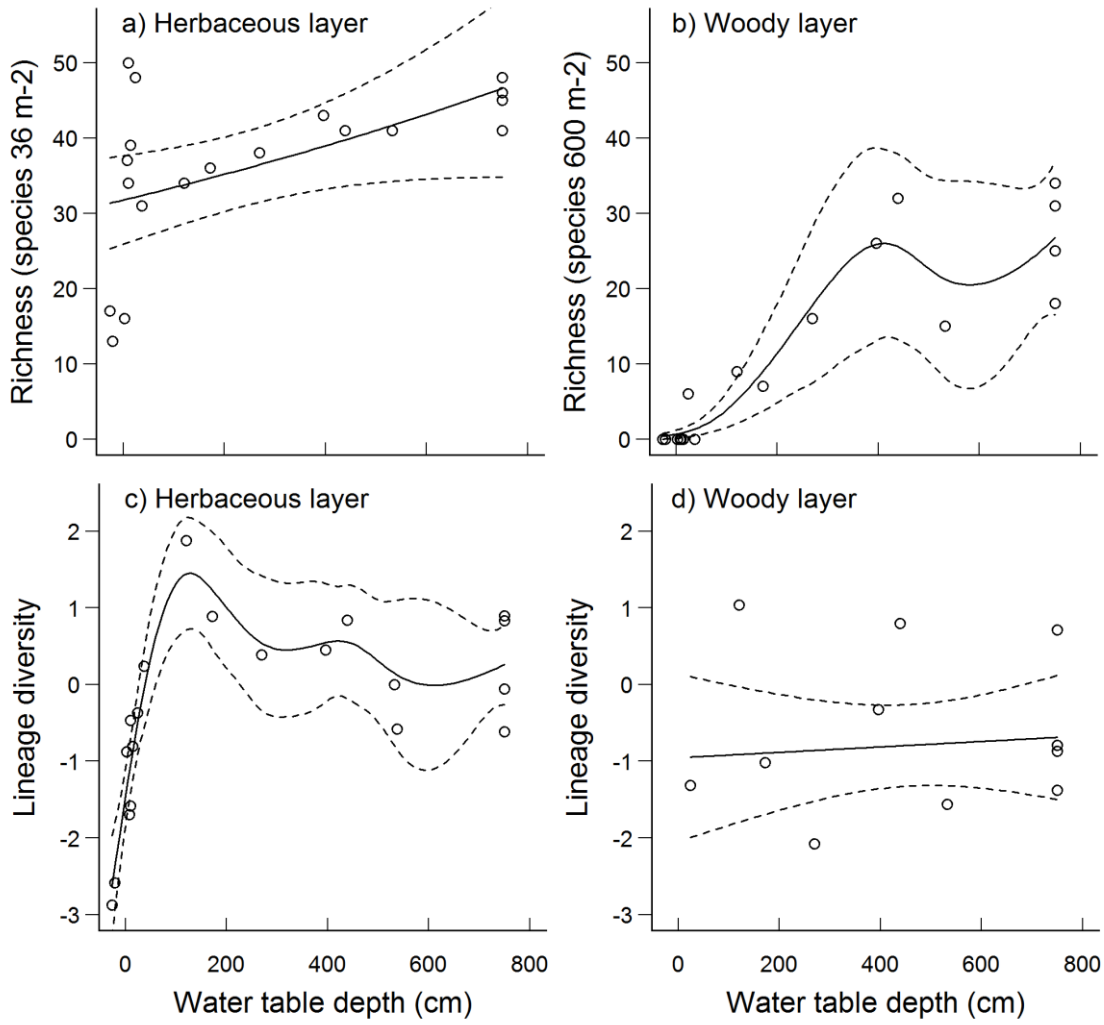
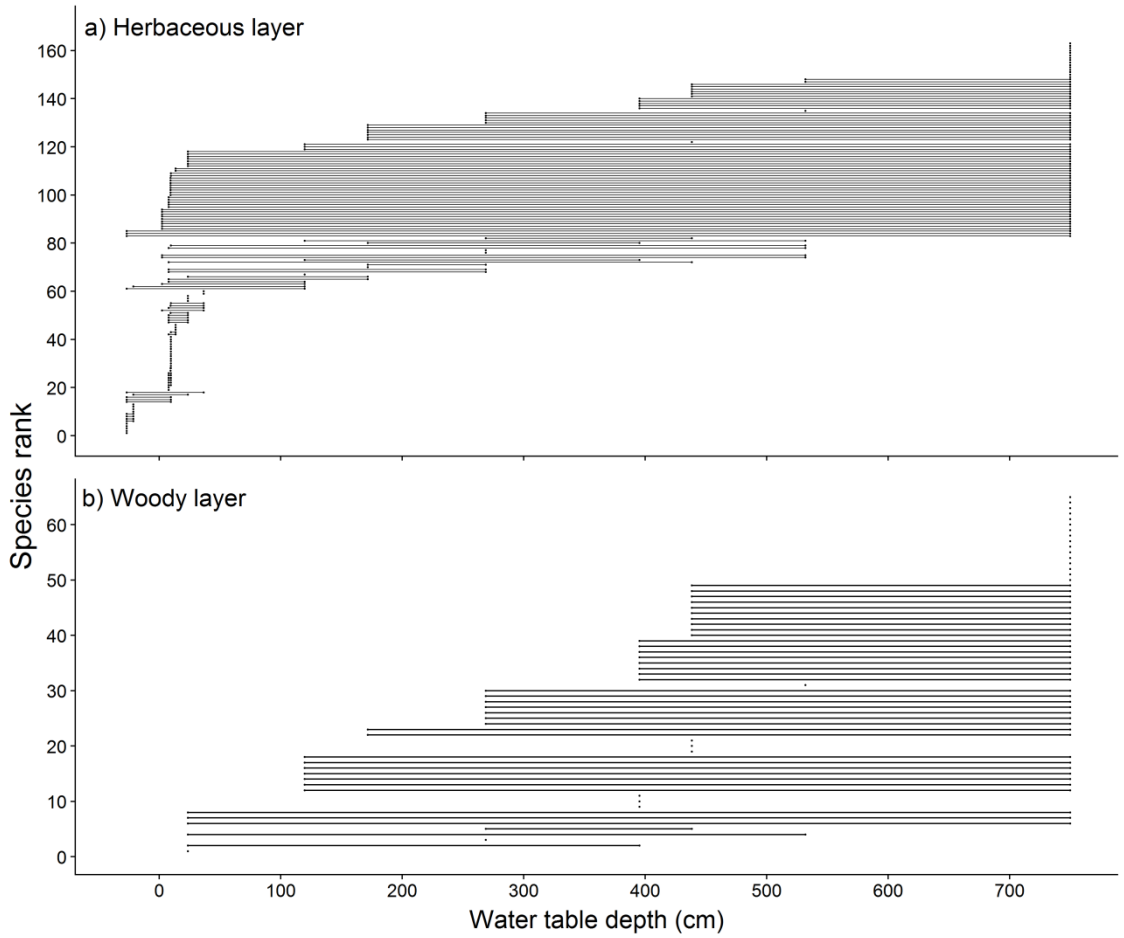

a) Herbaceous layer
b) Woody layer
c) Herbaceous layer
d) Woody layer
Richness (species 36 m-2)
Richness (species 600 m-2)
Lineage diversity
Lineage diversity
Water table depth (cm)
Water table depth (cm)
0
10
20
30
40
50
-3
-2
-1
0
1
2
0
200
400
600
800

Fig 3.


a) Herbaceous layer
b) Woody layer
Species rank
Water table depth (cm)
0
20
40
60
80
100
120
140
160
10
30
50
200
300
400
500
600
700